Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

PHYSIOLOGICAL CORRELATIONS AND CLIMATIC REACTIONS IN ALFALFA BREEDING[1]

GEO. F. FREEMAN

Arizona Agricultural Experiment Station

Climatic Reactions

To the worker who attempts to apply the recognized laws of heredity to the actual operations of plant improvement many difficulties arise which heretofore have been largely avoided by students of pure genetics. Color and form characters are but little affected by the immediate ordinary environment and hence, for the sake of simplicity, are usually chosen by investigators of heredity. To the economic breeder, however, such characters are of but little consequence except in so far as they indicate phyletic relationships. Of greater importance to the breeder are those differences in yield and quality which are the results of inherited, invisible, physiological powers within the plants, whereby each variety may respond differently in manner or degree to the same environmental stimulus.

Those hereditary units which have to do with vegetative vigor, heat, cold and drought resistance, time of maturity, chemical structure, reproductive strength, etc., are as yet but little understood. This is largely due to the difficulty of exact experiments concerning them. This difficulty is occasioned by the complexity of the reactions of these hereditary forces with the external environment, and also by the direct influence of the development of one part of the plant upon that of some other part. The plant at maturity presents the resultant of its environmental reactions during development. The nature of these reactions is determined by the structure of the vital forces within. These differences in vital structure may or may not be accompanied by visible morphological differences. Such cases of correlation have been known and used in selecting for qualities which they were thought to indicate. The much quoted example of the supposed correlation between the short-haired rachilla and high brewing quality in barley is a case in point. It has been found, however, that, whereas, in one strain or race the correlation may hold, in another, the two characters are in no way related. Another case of similar nature is the coupling of cob and pericarp color in certain varieties of corn and their complete independence in others. Many other examples could be adduced to show that the coupling of two characters in a given race of plants is no indication that these same characters are inseparably linked in all races of the same species. These facts have greatly reduced the value formerly ascribed to gametic correlations in plant breeding. Under our present knowledge, therefore, we must depend, for the most part, upon direct experimentation, rather than correlations, to discover the hereditary physiological characters of the varieties with which we are working. Any additional light, therefore, which may be had concerning the nature of such characters, together with methods for the study of the behavior of the same in their relation to each other and to their physical surroundings, will have not only a scientific value, but will also fill a distinct practical need.

---

[1] Read before the American Breeders' Association, Columbia, S. C., January 26, 1913.

As an illustration of such a study we may now examine the data concerning the development, yield and chemical composition of forty-four regional varieties of alfalfa which were grown on the Experiment Station Farm at Phoenix, Arizona, during the season of 1910. In the case of this plant, which occupies the ground throughout the year and from which six or seven crops may be harvested during the growing period, the climatic factors include a long series of variations coincident with the changing seasons. Now, since every variety consists of its own peculiar complex of hereditary physiological forces, each sensitive in its own manner and degree to the impinging external stimuli, it is not surprising that the resultant (the gross climatic reaction) should be sharply different in the several varietal groups.

The unequal effects upon the vegetative growth of the different varieties brought about by the climatic changes which occurred during the course of the summer may be exhibited by calculating the place variation in yield. This is best shown by correlating the first with each of the following cuttings throughout the season. The result is a definite curve, beginning and ending high with a strong sag in the middle.

TABLE I

PLACE VARIATION IN YIELD

Cuttings	1 and 2	1 and 3	1 and 4	1 and 5	1 and 6
Correlation.	+ .75 ± .04	+ .68 ± .05	+ .33 ± .09	+ .36 ± .09	+ .58 ± .07.

These figures indicate the presence of some disturbing factor which reached its maximum intensity during the fourth and fifth cuttings, and to which certain plots were more sensitive than others. The average period through which the growth of these two crops extended was June 22 to August 27. The fact that these dates include the hottest portion of the summer strongly suggests temperature as the disturbing factor.

The mean maximum temperature, mean minimum relative humidity and the correlation between yield and water supplied are given in the following table:

TABLE II

TEMPERATURE, RELATIVE HUMIDITY AND WATER SUPPLY

Cutting	Dates Including Average Periods of Growth	Mean Maximum Temperature ° F.	Mean Minimum Relative Humidity	Correlation Between Yield and Water Supply
1	From March 23 to April 23	82.8	27.00	
2	From April 23 to May 23	93.8	23.00	— .09 ± .10
3	From May 23 to June 22	103.6	20.40	+ .05 ± .10
4	From June 22 to July 23	104.8	25.26	+ .40 ± .09
5	From July 23 to August 27	104.4	30.00	+ .21 ± .10
6	From August 27 to October 5	102.0	25.18	— .04 ± .10

That the relative humidity had little to do with yield is shown by the fact that the highest averages for this factor occurred on the first and fifth cuttings which were the highest and lowest in yield, respectively.

Although it was intended to give each plot approximately the same amount of water for each cutting, unevenness in the slope made this impossible. The average amount of water applied to each cutting was 6.28 inches with an average standard deviation of 1.54 inches. Now, taking cognizance of this variation in the water supply, we find that its effect upon the yield was only appreciable in the fourth and fifth cuttings. Records were not made of the water supplied to the first cutting, but after that time they are complete. By reference to Table II it will be observed that these correlations in the second, third and sixth cuttings are so small as to be negligible, but in the fourth and fifth cuttings they are sufficiently large to indicate that this factor was of some importance in governing the yields. These results may be interpreted as meaning that approximately 6.28 inches of water were ample for each cutting during the cooler weather of spring and fall. That too much was not given at these seasons, however, is shown by the absence of large minus correlations. Factors other than water supply, therefore, governed the yields during these periods. Hot, dry weather came on during the growth of the third cutting, but the amount of water supplied plus the winter and spring surplus left in the soil was ample to mature the crop. With the continued high demand for water during the hot weather of July and August, the surplus having been exhausted and the summer rains helping but little, six and one fourth inches was not sufficient. There was, therefore, marked suffering for water, which was reflected in the yields of those plots that received slightly more or less of irrigation than the others.

It would seem, therefore, that high temperature and a slight deficiency of water were the disturbing factors in the relative yields of the varieties tested, and that certain ones were more sensitive than others to these influences.

If we turn to the relation between stand and yield, we shall again find a strong disturbance of the normal correlation as shown in the following:

TABLE III

CORRELATION BETWEEN STAND AND YIELD

Cutting	1st	2d	3d
Correlation	+ .78 ± .04	+ .55 ± .07	+ .47 ± .08
Cutting	**4th**	**5th**	**6th**
Correlation.	+ .54 ± .07	+ .10 ± .10	+ .70 ± .05.

The exceptionally low coefficient of the fifth cutting was due to the low yields on the part of plots which had good stands but were relatively inactive during the hot weather and partial water famine which occurred at this period. On the other hand, certain plots through their resistance to heat and consequent activity at this period, overcame to a large extent their handicap of poor stands, and nearly obliterated the usual plus correlation between stand and yield.

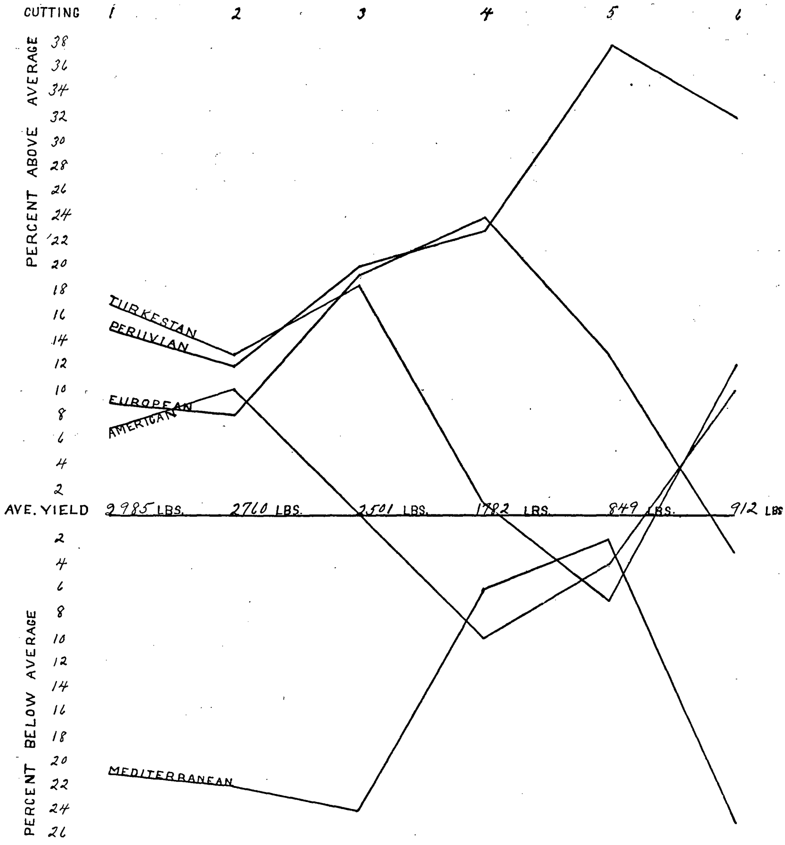
The data thus studied *en masse* indicate at least two physiological groups which are unequally sensitive to the climatic changes which occur in the course of a growing season, and whose reactions were sufficiently strong to change almost completely the order of the productivity of the plots. In order to test this conclusion let us turn to the individual plots and endeavor to discover and classify the physiological varieties indicated above.

If, now, we arrange the forty-four regional strains according to their morphological characters and geographical origin, we shall have five more or less distinct groups as follows: Mediterranean, Peruvian, European, American and Turkestan. The behavior of these varietal groups through the course of six cuttings during the summer of 1910 substantiates the conclusions already drawn and illustrates the sharp differences in climatic reactions which may be observed in the several varieties of a single species.

Morphologically the Mediterranean and Peruvian alfalfas are so distinct in type that any one at all familiar with the different kinds of alfalfa would recognize them at a glance, whether a whole field or a single plant be observed. The presence of yellow or greenish blue flowers also determines a variety to be of northern origin with mixtures of falcata characters, which usually carry with them resistance to cold and drought. Otherwise, the Turkestan, American and European types are so nearly alike that only an expert would recognize them in mass culture. The individual variations within these three types intergrade to such a degree that one could scarcely assume to judge, from the observation of a single plant, the type prevailing in the field from which it originated. The three types, however, differ markedly in their physiological reactions as we shall presently see. The distinctions, in this regard, as exhibited on our plots, are not nearly so marked between the American and Turkestan alfalfas as between these two types, on the one hand, and the European, on the other. However, in northern climates where winter resistance enters as a potent factor, the Turkestan alfalfa exhibits greater hardiness than the American form, and, therefore, is able to maintain a more perfect stand through seasons of extreme frost.

When grown under Arizona conditions, the average yields of each of these five type groups present seasonal curves at once striking in their diversity and contrasts. These differences are exhibited more easily by plotting the average of all the plots as a straight line, and the average of the different groups as percentages of the total average above and below the general average line.

In observing Fig. 1, we are first impressed with a marked similarity in the performance of the European and Mediterranean alfalfas, on the one hand, and the American and Turkestan on the other, and also with the striking differences exhibited between the two groups. Although the average yield of the European plots greatly exceed that of the Mediterranean plots, the shapes of their respective curves are almost exactly alike, the greatest relative yield of each being in the heated part of the summer after the beginning of the water famine. In like manner, the American and Turkestan varieties made similar relative yield curves, that for the Turkestan being slightly above the curve for the American strains. Here, however, the



Relative Yield of Regional Varieties Based on the Average of All Plots as 100 Per Cent.

curves bend strongly downward in mid and late summer, as if these types were much less resistant to the accumulative effects of drought and heat. In fact, it would seem that during the hot period included within the fifth cutting

(July and August), the American and Turkestan varieties were comparatively inactive, yielding only about eight hundred pounds of dry hay per acre, as against more than a ton and a half each on the first cutting. The relative yield curve for the Peruvian type stands separate and distinct from the others. Although here, as with other varieties, the yield declines with the advance of the season, the persistence and vigor with which this strain resisted the summer heat and drought caused it to gain rapidly on the other varieties in relative yield throughout the season until the very last cutting, when there was a slight decline.

Disregarding the shape of the curves we may now notice the total yield for the season. In this respect the different regional varieties take the following relative order: Peruvian, European, Turkestan, American and Mediterranean. It is here noticeable that, though the European and Mediterranean varieties have similar seasonal yield curves, they are not contiguous in the arrangement based on total yields. This is a result of a marked difference in the stand maintained by the two varieties which averaged ninety-two per cent. for the former and seventy-four per cent. for the latter. In their ability to maintain stand, the Peruvian, European, Turkestan and American varieties were about equal, averaging 92, 92, 93 and 94 per cent., respectively. The lack of stand on the part of the Mediterranean alfalfas was not due to the poor quality of the original seed, for all of these plots once had perfect stands. This behavior is also in accordance with the records of other fields of Mediterranean alfalfa in the southwest, which have come under the observation of the writer. The explanation of the weakness of the Mediterranean and corresponding strength of the otherwise similarly reacting European alfalfa in maintaining stand under Arizona conditions is a subject for further careful physiological study.

The recognition, analysis, and calibration of these differences of the physiological reactions of varieties are thus seen to become a first essential in the study of climatic adaptation, and form the basis for rational procedure in the choice of varieties and in selective breeding for the improvement of the same.

CORRELATIONS

In the improvement of varieties of plants, quality is often as important as quantity of yield. This is especially true in a forage crop, such as alfalfa. Since nitrogen, next to fat, is the most expensive of the necessary food constituents, it may be taken as the measure of quality. Commerical buyers judge alfalfa hay by its purity, odor, color and percentage of leaves retained in curing and baling. The value of the leaves lies in their relatively high nitrogen content and the consequent increased food value which they impart to the hay. Expressed quantitatively, the correlations between the nitrogen content of the hay and the percentage of leaves for the six cuttings were as follows:

TABLE IV

CORRELATION BETWEEN NITROGEN CONTENT OF HAY AND PER CENT. OF LEAVES

Cutting	1st	2d	3d
Correlation	+ .46 ± .08	+ .61 ± .06	+ .72 ± .05
Cutting	4th	5th	6th
Correlation	+ .68 ± .05	+ .61 ± .06	+ .52 ± .07.

That the final value of the hay is markedly dependent upon the composition as well as the percentage of leaves is shown by the following high and fairly uniform correlation between the nitrogen content of the hay and the nitrogen content of the leaves:

TABLE V

CORRELATION BETWEEN NITROGEN CONTENT OF HAY AND NITROGEN CONTENT OF LEAVES

Cutting	1st	2d	3d
Correlation	+ .69 ± .05	+ .73 ± .05	+ .42 ± .08
Cutting	4th	5th	6th
Correlation	+ .67 ± .06	+ .85 ± .03	+ .74 ± .05.

If, now, we have shown that the quality of the hay depends primarily upon the percentage and composition of the leaves, we may proceed to investigate those factors which indirectly modify the feeding value by influencing the amount or character of these organs.

The factors most profoundly affecting the percentage of leaves were yield, height and stage of maturity at which the cutting was made. Local or varietal forces were sufficiently constant to hold the place variation of this character to the plus side of the equation for four out of five determinations made, as is seen in the following table:

TABLE VI

PLACE VARIATION IN PERCENTAGE OF LEAVES

Cutting	1 and 2	2 and 3	3 and 4	4 and 5	5 and 6
Correlation.	+ 10 ± .10	+ .23 ± .10	+ .16 ± .10	+ .46 ± .08	— .12 ± .10.

These correlations, however, are low and seem to indicate that the natural varietal traits were being overcome and obscured by other variable factors.

Contrary to expectation, the stand had little to do with the percentage of leaves, as the following low and inconstant correlations show.

TABLE VII

CORRELATION BETWEEN THE PERCENTAGE OF LEAVES AND STAND

Cutting	1st	2d	3d
Correlation	— .14 ± .10	— .02 ± .10	+ .03 ± .10
Cutting	4th	5th	6th
Correlation	+ .10 ± .10	+ .07 ± .10	+ .24 ± .10.

On the other hand, the relation between height and yield and percentage of leaves was constant and marked, except in the last two cuttings.

TABLE VIII

CORRELATION BETWEEN PERCENTAGE OF LEAVES AND HEIGHT AND YIELD

Cutting	1st	2d	3d
Yield	— .41 ± .08	— .60 ± .07	— .15 ± .10
Height	— .48 ± .08	— .62 ± .06	— .68 ± .05
Cutting	4th	5th	6th
Yield	— .40 ± .09	+ .20 ± .10	+ .30 ± .09.
Height	— .55 ± .07	+ .09 ± .10	+ .19 ± .10.

The sudden change from minus to plus in these correlations should be noted. The average heights of the first four cuttings were 32, 30, 28 and 27 inches, respectively. The average height of the fifth and sixth, were 15 and 12 inches. This would suggest that at or below 15 inches the mutual shading of the stems is not sufficient to cause an appreciable shedding of the lower leaves. Up to this point, moreover, growth usually takes place by an increase in the number of nodes, each with its accompanying leaves and side branches. Above fifteen inches, however, the principal growth in height consists in a lengthening of the internodes and, consequently, a relatively greater production of stem as compared with leaf tissue. In this physiological correlation lies the core of the difficulty in breeding at once for quality and quantity. The act of high production within itself cuts down the quality of the product by reducing the ratio between the leaves and the stems.

This difficulty, moreover, occurs in the composition as well as the percentage of the leaves. The correlation existing between the nitrogen content of the leaves and the number of days required to mature a cutting is shown in the following table:

TABLE IX

Correlation between the Nitrogen Content of Hay and the Period Required for Maturity

Cutting	1st	2d	3d
Correlation	—.33 ± .09	—.30 ± .09	—.27 ± .09
Cutting	4th	5th	6th
Correlation	—.52 ± .07	—.50 ± .08	—.17 ± .10.

Quickly maturing varieties thus have leaves richer in nitrogen than those which require a greater length of time for completion of growth. When, however, we take the average number of days required throughout the season to mature a cutting for each plot and compare this with the total seasonal yield we find a correlation of + .43. Thus we are again confronted by a minus correlation between quality and yield which must be overcome if we would make progress simultaneously in both lines.

As further examples of antagonistic correlations, a few instances may be taken from the data furnished by forty-three plots of pure races of alfalfa grown during the summer of 1910. The correlation between height and percentage of leaves was again constant and marked. The results here paralleled those found for the regional varieties. Whereas yield was uniformly correlated positively with both stooling capacity (av. No. stems per plant) and height, it is interesting to note that there was also a uni-

TABLE X

CORRELATION IN PURE RACES

Correlation Between	Cuttings			
	July	August	September	October
Green weight and average number stems	+ .75 ± .04	+ .42 ± .08	+ .62 ± .06	+ .50 ± .08
Green weight and average height	+ .01 ± .10	+ .44 ± .08	+ .22 ± .10	+ .33 ± .09
Average height and number of stems	— .29 ± .09	— .19 ± .10	— .32 ± .09	— .21 ± .10
Average height and per cent. leaves	— .39 ± .09	— .15 ± .10	— .55 ± .07	— .51 ± .08

form minus correlation existing between them. We thus have two factors both making for yield, but seemingly (probably physiologically) antagonistic to each other. In breeding for high yielding strains we are here again called upon to overcome by selection an antagonistic physiological correlation.

This brings us to the following final conclusion which the writer wishes to emphasize:

In economic plant breeding one frequently encounters physiologically negative correlations such as those, in alfalfa, between height and stooling capacity, height and percentage of leaves, and between yield and quality. In seeking improvement, therefore, the breeder must recognize and make use of these facts in the interpretation of results obtained, and also search for races which violate such naturally antagonistic correlations to the greatest possible extent.

GENERAL CONCLUSIONS

That the complex of allelomorphs, which we call a variety, may be definite as both to ultimate composition and organization is not here questioned. When, however, we consider that visible characters are only the expression of the reactions of the vital forces of the plant with the environment, we can realize that the variety, as we see it, is not a definite thing, but is a result of two independent classes of factors. Change either and the result correspondingly changes.

We are therefore to look upon the variety as a delicately organized chemical compound. The various factors of climate and soil may be compared to different physical influences to which the original compound may be subjected. As the chemist would expect reactions varying in accordance with the physical stimuli used, so will the plant react in agreement with the different environmental combinations. The extent to which this will change the nature and appearance of plants is often far reaching. Cook, working with cotton, has found that certain cultural conditions at an early stage of growth will make profound differences in the method of branching which determines the whole subsequent development of the plant and affects materially its economic value. Cultural and climatic reactions often lead to error among those who assume them to be mutative changes induced by the new conditions. That these reactions may bring to light sub-races with hereditary tendencies not hitherto called into expression and which, by selection, may be secured as pure races, is the probable explanation of many cases of supposed direct climatic adaptation.

Thus, realizing the true nature of a variety, we can draw further upon the analogy of the chemist who investigates an unknown substance by testing its reactions with a large number of known reagents. In like manner the breeder can only understand the true nature of the hereditary vital forces within a plant after he has tested and calibrated its reactions against a variety of soil and climatic factors. These reactions are of interest to the farmer only in so far as they affect the economic value of the variety as grown in his own locality but to the breeder and student of heredity their importance is fundamental. This is so because they enable him to classify, coordinate and interpret the experimental results that he obtains. This ability finally must form the basis of all rational procedure, whether one be engaged in the study of pure genetics or in the operations of practical plant improvement.